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COLOR INHERITANCE IN LYCHNIS DIOICA L.[1]

DR. GEORGE HARRISON SHULL

Two years ago I showed that in *Lychnis dioica* L. the purple-flowered form behaves in normal Mendelian manner when crossed with the same type or with the typically white-flowered form of the same species (Shull, 1908). In subsequent work it has been discovered that the purple-flowered plants do not form a single unit-group, but that there are at least two distinct types, one of which has more bluish-purple flowers, the other more reddish-purple. No notice had been taken of such variation in the color characters until last year, although it had been observed that there was some variation in the intensity of color in different plants, and these had been, to a slight extent, recorded in terms of intensity, *e. g.*, as "light," "medium" and "dark." Last year several individuals were observed so noticeably distinct because of the bluish character of their flowers, that an effort was made to determine the relationship of this light bluish-purple color to the more common reddish-purple, and several crosses were made representing the combination of "blue" and "red," using a single red-flowered indi-

TABLE I

Ped. No.	Cross.	Red.	Blue.	White.	Theoretical Result.	Ratio Involved.
0845	Blue × Blue	1	83	0	0 : 84 : 0	0 : 1 : 0
0846	Blue × Red	47	49	0	48 : 48 : 0	1 : 1 : 0
0844	Blue × White	52	0	46	49 : 0 : 49	1 : 0 : 1
0849	Red × Red	68	22	1	68 : 23 : 0	3 : 1 : 0
0848	Red × Blue	27	32	27	32 : 32 : 22	3 : 3 : 2
0847	Red × White	53	0	46	50 : 0 : 49	1 : 0 : 1
0875	White × Blue	34	24	41	25 : 25 : 49	1 : 1 : 2
0876	White × Red	31	20	0	38 : 13 : 0	3 : 1 : 0
	Total	313	230	161	310 : 225 : 169	

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[1] Read before the Botanical Society of America at Boston, December, 1909.

vidual as the mother in one series of crosses, and a single blue-flowered individual as the mother in another series. The same blue-flowered and red-flowered plants were also crossed at the same time with white-flowered plants. The actual and theoretical results of these eight crosses are given in Table I.

In addition to these families which were bred in such a way as to allow the definite working out of the gametic formulæ of the parents and the theoretical results, bluish-flowered plants were also observed in a number of other pedigrees. In some of these families only a small proportion of the individuals had their tints recorded, as they were being especially studied with other objects in view. Such fragmentary records are of no special value in this connection, of course, and they will not be presented, but in Table II. are given all those pedigrees in which approximately all the purple-flowered offspring were recorded either as "blue" or "red."

In this second table it is impossible to vouch for the correctness of the suggested theoretical results, as the gametic formulæ of the parents are in each case very imperfectly known. The column of theoretical results is constructed simply by using that one of the available theoretical ratios which fits most accurately the observed facts. When numbers are so small, mere inspection can not determine with certainty which is the correct theoretical ratio. Thus in No. 08168 the empirical ratio, 19:11:31, is almost equally well referred to either of the available ratios, 1:1:2 and 3:1:4, as it stands about midway between them. Notwithstanding the fact that ignorance of the gametic composition of the parents in this second table makes it impossible to decide in all cases what ratio should have been expected, the results harmonize well throughout with those which comprise Table I., where the theoretical "expectation" is definitely known.

All of the crosses recorded in these two tables seem to be typically Mendelian, with the bluish-purple color hypo-

TABLE II

Ped. No.	Cross.	Red.	Blue.	White.	Probable Theoretical Result.	Ratio Invoked.
0850	Red × Red	67	0	0	67 : 0 : 0	1 : 0 : 0
0851	Red × White	40	13	0	40 : 13 : 0	3 : 1 : 0
0852	White × Red	26	4	52	23 : 8 : 51	9 : 3 : 20
0853	Red × Red	82	0	19	76 : 0 : 25	3 : 0 : 1
0855	Red × Red	105	0	0	105 : 0 : 0	1 : 0 : 0
0856	Red × White	39	18	39	36 : 12 : 48	3 : 1 : 4
0857	Red × Red	64	14	25	58 : 19 : 26	9 : 3 : 4
0858	Red × White	17	12	33	16 : 15 : 31	1 : 1 : 2
0859	Red × White	10	0	14	9 : 0 : 15	3 : 0 : 5
0860	Red × Red	77	0	21	74 : 0 : 24	3 : 0 : 1
0861	Red × White	38	0	0	38 : 0 : 0	1 : 0 : 0
0862	Red × Red	101	0	0	101 : 0 : 0	1 : 0 : 0
0863	Red × Red	30	0	6	27 : 0 : 9	3 : 0 : 1
0864	Red × White	3	0	13	4 : 0 : 12	1 : 0 : 3
0865	White × Red	18	0	6	18 : 0 : 6	3 : 0 : 1
0866	White × Red	37	0	29	33 : 0 : 33	1 : 0 : 1
0867	White × Red	25	0	16	20 : 0 : 21	1 : 0 : 1
0868	Red × Red	74	0	12	65 : 0 : 21	3 : 0 : 1
0869	Red × White	44	0	49	47 : 0 : 46	1 : 0 : 1
0871	White × Red	30	0	54	31 : 0 : 53	3 : 0 : 5
0882	White × Red	23	8	43	21 : 7 : 46	9 : 3 : 20
0884	White × Red	26	8	40	28 : 9 : 37	3 : 1 : 4
08100	White × Red	44	0	45	44 : 0 : 45	1 : 0 : 1
08105	White × Red	29	0	29	29 : 0 : 29	1 : 0 : 1
08150	Red × White	23	27	35	21 : 21 : 43	1 : 1 : 2
08155	Red × Red	25	0	0	25 : 0 : 0	1 : 0 : 0
08156	White × Red	29	16	34	30 : 10 : 39	3 : 1 : 4
08161	Red × Red	44	13	18	42 : 14 : 19	9 : 3 : 4
08162	Red × White	48	0	45	47 : 0 : 46	1 : 0 : 1
08168	White × Red	19	11	31	15 : 15 : 31	1 : 1 : 2
08175	Red × Red	70	0	29	74 : 0 : 25	3 : 0 : 1
08177	Red × Red	72	0	22	71 : 0 : 23	3 : 0 : 1
08178	Red × White	47	0	47	47 : 0 : 47	1 : 0 : 1
	Total	1,426	144	806	1,382 : 143 : 851	

static or "recessive" to the red. This is one of the first cases of this kind which has appeared, as heretofore the bluish colors have quite generally been found epistatic to the reds. The most important studies which have been made relating to the inheritance of the anthocyan colors are those of Bateson (1902, 1905, 1906, 1909) and his co-workers, on *Lathyrus* and *Matthiola,* Miss Wheldale (1907) and Baur (1908) on *Antirrhinum,* and Tschermak (1901, 1904) on *Pisum* and *Phaseolus.* In all of these genera as well as in *Clarkia* and *Salvia* (Bateson, etc., 1905), the more bluish anthocyan color is epistatic to the reddish anthocyan. Bateson (1909, p. 41) states in one place, that in *Primula Sinensis* "blue is hypostatic to all the red shades,'' although the magenta colors are shown to be epistatic to red. This isolated statement regarding the blue color in *Primula Sinensis* is not supported by any data, and I do not know the chemical relation between it and the magenta colors. Miss Wheldale (1909), who discusses at some length the color series in *Primula* material secured from Bateson and Gregory, makes no mention of the occurrence of blue, though she ascribes the production of magenta and crimson to the action of a ''bluing factor'' upon red anthocyan.

Upon comparison of my bluish-purple *Lychnis* with the colored plates of *Primula* given by Bateson (1909, p. 294) I think the *Lychnis* color should be classed as a light magenta rather than a blue, as there is a decided reddish element in this *Lychnis* color. If Bateson's isolated statement that ''blue is hypostatic to all the red shades'' in *Primula* is correct, then that color corresponds in its behavior with this light magenta color in *Lychnis*. I have not made a thorough investigation of the chemical relations of the two types of purple in *Lychnis*, but have demonstrated by a few preliminary tests that the reddish-purple color is converted to bluish when treated with alkalies, and that the light bluish-purple is made as bright red as the red-purple type on treating with weak acids, thus indicating a very simple relation between these two colors.

Although the relation between the two types of color in *Lychnis* is just the reverse of that exhibited by practically all other plants in which similar colors have been studied, I am led to essentially the same conclusions regarding the method of color determination, as those derived from the extensive studies which have been made on *Lathyrus*, *Matthiola*, etc. The production of the ''lowest stage'' of color, *i. e.*, the color which results from the combined action of the least number of genes, is due to the interaction of two independent factors or genes, either of which produces no color when not associated with the other. In order to produce a second stage of color it is necessary to assume the occurrence of a third gene which can make its characteristic color-reaction apparent only in the presence of the other two. Thus in *Lathyrus*, etc., it was assumed that two factors, *R* and *C*, are necessary to the production of a red anthocyan color, and that a third factor, *B*, modifies this color to bluish. This assumption requires that the presence of each of these three genes be dominant over its absence. An alternative assumption might have been made, viz., that the absence of the third factor is dominant over its presence. Then the lowest grade of color would be a *blue* color produced by the simultaneous presence of *B* and *C*, and the red color would appear only when *R* is present in the homozygous state.

Last year in my discussion of the presence and absence hypothesis (Shull, 1909) it was pointed out that it would be impossible in many cases to determine "whether red flowers are blue flowers with an added factor for acidity or whether blue flowers are red with an added factor for alkalinity," and also that "it is conceivable that both these situations may be presented in different species." The color characters in *Lychnis* give a very good illustration of these statements.

If we assume the dominance of presence over absence, the lowest grade of color—the bluish—is formed by the combined action of two genes, *B* and *C*, the one probably representing, according to the studies of Miss Wheldale (1909), the capacity to produce a chromogen of the flavone series, the other representing the production of an oxidase. The red color is in this case produced by an added factor, *R*, which modifies the bluish color produced by *B* and *C*. The *R* may be perhaps an acidifier, a reducing agent, or a partial inhibitor of the oxidizing action of *B*. This method of explaining color inheritance in *Lychnis* presents an interesting reversal of the places occupied by *R* and *B* when compared with the situation in other plants.

If, on the other hand, the assumption be made that, in *Lychnis,* absence of B is dominant over its presence, the relative positions of R and B may remain the same as in *Lathyrus, Matthiola,* etc. For in this case R and C will be the two factors necessary to the production of red anthocyan and B the "bluing factor" which is added to it to form bluish anthocyan, the difference between *Lychnis* and *Lathyrus* being simply that the B which may be looked upon perhaps as a factor for alkalinity or for an oxidizer, is too weak in its activity in *Lychnis* to produce its characteristic effect except when present in double quantity or strength, as it is when in the homozygous state.

The data now at hand do not make possible a decision as to whether presence, or absence of the color-modifier, is dominant in *Lychnis,* as each of these assumptions may be shown to fit all the facts involved in Table I. The gametic formulæ of the six plants involved in these eight crosses are presented in Table III., to enable a comparison of the two methods of explanation.

TABLE III

Ped. No.	Crosses.	$B + C$ Produces Blue. Presence of R Dominant.	$R + C$ Produces Red. Absence of B Dominant.	Resultant Ratio Red : Blue : White.
0845	Blue × Blue	$BCC \times BBC$	$BBRCC \times BBRRC$	0 : 1 : 0
0846	Blue × Red	$BCC \times RBBCC$	$BBRCC \times BRRCC$	1 : 1 : 0
0844	Blue × White	$BCC \times RR\ (CC?)$	$BBRCC \times CC$	1 : 0 : 1
0849	Red × Red	$RB(B?)C \times RBBCC$	$BRC \times BRRCC$	3 : 1 : 0
0848	Red × Blue	$RB(B?)C \times BBC$	$BRC \times BBRRC$	3 : 3 : 2
0847	Red × White	$RB(B?)C \times RR(CC$ if $♀ = RBC)$	$BRC \times CC$	1 : 0 : 1
0875	White × Blue	$RB(B?) \times BBC$	$B \times BBRRC$	1 : 1 : 2
0876	White × Red	$RB(B?) \times RBBCC$	$B \times BRRCC$	3 : 1 : 0

The fact now demonstrated that the purple color in *Lychnis* is due to the presence of at least three distinct genes instead of only one, as originally assumed by me, has served to elucidate several difficulties which had been encountered. It may be recalled that a rather large range of supposedly fluctuating variability in the percentage of purple-flowered individuals in families resulting from crosses of purple with white was shown to form a normal probable error curve, thus conforming very well with the Mendelian hypothesis that gametes of different alternative composition unite according to the laws of chance. While this conclusion is not in any way opposed by my later studies, it is now known that a portion of that apparently fluctuating variation may have been due to the occurrence of a mixture of several different ratios. In accordance with the present demonstration that the purple color is due to three factors, the combined action of two of which are necessary to the production of any color and the addition of a third for the modification of this color, a cross between white and purple must give either all purple, or purple and white in any of the following ratios: 3:1, 1:1, 3:5, or 1:3, though the ratio 1:1 occurs much more frequently than any of the other possibilities. In other words, without any fluctuation at all, purple-flowered individuals, when mated entirely at random with white-flowered individuals, should produce progenies consisting of 25, 37.5, 50, 75 or 100 per cent. purple-flowered offspring, instead of only 50 or 100 per cent.

I have in several cases found purple-flowered individuals among the offspring of two white-flowered parents. Such occurrence was entirely incomprehensible to me except on the basis of an error in technique. It now becomes obvious that white crossed with white must occasionally give various proportions of purple-flowered offspring. Some such crosses will give all purple while others will give purple and white in ratios 1:1, 3:5, or 1:3, although a frequent result will be a progeny of all white, which latter alone was expected under the conception that the purple color was due to the presence of a single gene. Although I have reared many families in which both parents were white, I have almost invariably obtained a progeny of all whites, but this is undoubtedly due to the fact that such crosses of white with white were nearly always made between sibs in wholly white-flowered families. Such crosses are necessarily homozygous with respect to the absence of one (or both) of the two genes whose joint action is necessary to the production of color. Crossing of white-flowered individuals of different parentage or of white sibs in hybrid families will doubtless quickly demonstrate the production of purple-flowered offspring by white-flowered parents, in the ratios required by theory.

Summary

The purple color in *Lychnis dioica* L. is a compound character, produced by the interaction of three distinct and independent genes in a manner exactly analogous to the similar colors in *Lathyrus, Matthiola,* etc.

The two types of purple color present in different individuals are a reddish and a more bluish-purple, the former being changed to blue by treatment with alkalies, and the latter changed to red by the addition of weak acids.

The bluish or alkaline color is hypostatic to the reddish or acid color, this being the reverse of the condition found in all other plants containing similar series of colors which have thus far been reported, unless possibly an isolated statement should prove correct that in *Primula Sinensis* "blue is hypostatic to all the red shades."

It is impossible to determine at present whether this reversal of the relation between bluish and reddish anthocyan results from the occurrence of positive characters for both alkalinity and acidity, or whether only one of these exists as a positive character and the alternative color is produced when this positive color-modifier is in the heterozygous state, the latter situation involving the dominance of absence over presence.

The rather wide fluctuation in the percentage of purple-flowered families resulting from the cross of heterozygous purple with white (*i. e.,* supposedly $DR \times R$), reported in a former paper, may have been due in part to the mixture of the ratios 3:1, 1:1, 3:5 and 1:3, all of which are expected Mendelian results, on the basis of present knowledge of the compound character of *Lychnis* colors.

Crosses between white-flowered plants should, not infrequently, result in progenies of all purple-flowered offspring or of purple and white in the ratios 1:1, 3:5, or 1:3. These results have not yet been found, owing no doubt to the fact that my crosses between white and white have been almost invariably made between sibs in wholly white-flowered families.

STATION FOR EXPERIMENTAL EVOLUTION,
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